Genetic parameter estimates of early growth traits in the Tygerhoek Merino flock

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Abstract

Genetic parameters were estimated for birth weight (BWT), weaning weight (WWT) and pre-weaning average daily gain (ADG) using Restricted Maximum Likelihood (REML) procedures. Four different animal models were fitted, differentiated by including or excluding maternal effects. The direct heritability estimates (h^2) ranged from 0.19 to 0.38, 0.25 to 0.36 and 0.26 to 0.34 for BWT, WWT and ADG, respectively. The estimates were substantially higher when maternal effects, either genetic or environmental, were ignored from the model. The maternal heritability (m^2) for BWT was 0.38 when only maternal genetic effects were fitted in the model but decreased to 0.25 when the maternal permanent environmental effect (c^2) was fitted. The m^2 for WWT and ADG ranged from 0.05 to 0.11 and from 0.04 to 0.10, respectively. The respective c^2 estimates ranged from 0.06 to 0.10 and from 0.06 to 0.09. Moderate negative genetic correlations (r_{am})between direct and maternal genetic effects were observed in BWT, while close to zero estimates were obtained for WWT and ADG. The direct genetic correlation estimates between BWT and WWT and BWT and ADG were 0.16 and 0.04, respectively. The corresponding maternal genetic correlation estimates were 0.93 and 0.60. The direct and maternal genetic correlation estimates between WWT and ADG were 0.99 and 0.85, respectively. It is suggested that selection should be applied to WWT.

Keywords: Early growth, direct heritability, maternal effects, genetic correlation, Merino sheep
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Introduction

Estimates of genetic parameters such as heritabilities and genetic correlations for early growth traits are important in the design of appropriate breeding programmes aimed at maximizing genetic improvement. They provide an indication of the relative genetic importance of traits, as either direct genetic response or correlated response to selection.

In mammals, growth is influenced by the genes of the individual for growth, by the environment provided by the dam and other environmental effects (Lewis & Beatson, 1999; Albuquerque & Meyer, 2001). In young animals, the milk supply of the dam and the maternal care she provides largely contribute to their growth (Bradford, 1972; Lewis & Beatson, 1999). The dam's genes for these traits affect the environment experienced by the offspring through milk production and mothering ability (Bourdon, 2000). Maternal effects may be expected to be more important in sheep than in cattle because of the greater relative variation in litter size in sheep and the competition between lambs for their mother's milk supply. It incorporates both similarities between twins and similarities between lambs born to the same ewe in different years (Snyman *et al*., 1995).

The confounding of the maternal effect of the dam and her genetic contribution to the phenotypic value of her offspring and the possibility of a negative genetic correlation between the direct and maternal effect are important problems in selection programmes (Willham, 1980). Thus, in order to decide upon a feasible selection strategy, estimation of the genetic parameters and the correlations between direct and maternal genetic effects is necessary.

To determine the effectiveness of breeding programmes, genetic trends in the population under consideration can be monitored (Van Wyk *et al.*, 1993b). According to Wilson & Willham (1986), trend lines may be used to compare alternative methods of selection or management. So far, no genetic trends have been estimated for early growth traits in the Merino flock at the Tygerhoek Experimental Farm. Moreover, a lack of estimates for birth weight was identified by Cloete *et al.* (2001).

The objectives of this study were to estimate genetic parameters for birth weight, weaning weight and average daily gain to weaning and to estimate genetic trends for these traits in the Tygerhoek Merino flock.

Materials and Methods

Records of 8310 lambs born from 2538 ewes and sired by 681 rams, raised over the period from 1970 to 1998 were used in this study. The general management of the flock and description of the study area are as described by Heydenrych *et al*. (1984) and Cloete *et al*. (1992). Liveweight at birth (BWT), weaning (WWT) and pre-weaning average daily gain (ADG) were the growth traits investigated. Lambs were weaned at approximately 120 days of age from 1970 to 1982, and at about 100 days of age thereafter, and WWT was adjusted accordingly for all lambs.

The General Linear Model (GLM) procedures of SAS (1996) were used to determine whether any of the effects or their interactions have an influence on the traits ($P < 0.05$). Those having an effect ($P < 0.05$) were fitted in the subsequent models to estimate the genetic parameters. Fixed effects fitted were lambing year (1970 to 1998), sex (male, female), birth type (single, multiple), dam age (2 to 6-yr old age), group of animals (group of animals selected for increased clean fleece weight and unselected control group), the lambing year by group interaction and lambing year by type of birth interaction.

Genetic parameters were estimated by Restricted Maximum Likelihood procedures (REML) applying the VCE 4.2.5 package of Groeneveld (1998). Unitrait genetic analyses were conducted for all three traits. Four different animal models were fitted, differentiated by either including or excluding the maternal effects. By using estimated (co)variance components, direct heritabilities (h^2), maternal heritabilities (m^2), maternal permanent environmental variances (c^2) and the correlations between the direct and maternal genetic effects (r_{am}) were obtained. Total heritabilities (h^2_t) were calculated as defined by Willham (1972) for those analyses where maternal genetic effects were obtained. All models included the same fixed effects. Genetic correlations among growth traits were subsequently obtained by using multitrait analyses, fitting all three traits simultaneously on Model 1 only.

The models were:

1. $Y = X\mathbf{b} + Z\mathbf{a} + e_{ijklm}$ (Model 1)
2. $Y = X\mathbf{b} + Z\mathbf{a} + P\mathbf{c} + e_{ijklm}$ (Model 2)
3. $Y = X\mathbf{b} + Z\mathbf{a} + M\mathbf{m} + e_{ijklm}$ $\quad Cov\ (a, m) = A\sigma_{am}$ (Model 3)
4. $Y = X\mathbf{b} + Z\mathbf{a} + M\mathbf{m} + P\mathbf{c} + e_{ijklm}$ $\quad Cov\ (a, m) = A\sigma_{am}$ (Model 4)

where:

- Y = the vector of records
- **b** = the vector of fixed effects
- X = the matrix that associates **b** with Y
- **a** = the vector of breeding values for direct genetic effects
- Z = the matrix that associates **a** with Y
- **m** = the vector of breeding values for maternal genetic effects
- M = the matrix that associates **m** with Y
- **c** = the vector of permanent environmental effects due to the dam
- P = the matrix that associates **c** with Y
- **e** = the vector of residual effects.

Further, with **A** the numerator relationship matrix between animals, $\mathbf{I}_n$ an identity matrix with order the number of animals and **I** an identity matrix with order the number of records, the (co)variance structure of the random effects in the analysis can then be described as: $V(a) = \sigma^2_a \mathbf{A}$, $V(m) = \sigma^2_m \mathbf{A}$, $V(c) = \sigma^2_c \mathbf{I}_n$, $V(e) = \sigma^2_e \mathbf{I}$ and $Cov(a, m) = \mathbf{A}\sigma_{am}$, where σ^2_a is the direct genetic variance, σ^2_m, the maternal genetic variance, σ^2_c, the maternal permanent environmental variance, σ^2_e, the residual variance and σ_{am}, the genetic covariance between the direct and maternal effects. It was assumed that all effects in the models are independent with the exception of the direct and maternal genetic effects.

In estimating the genetic trends, breeding values of animals for BWT and WWT, both for the direct and maternal genetic effects, estimated from Model 3, were used. Aggregate breeding values, which is the sum of the direct and maternal breeding values (Azzam & Nielson, 1987), were calculated

for both traits. The breeding values of animals born within specific years (age contemporaries) were averaged and subsequently regressed on years to obtain the genetic trends over years.

Results

Estimates of (co)variance components, direct (h^2) and maternal (m^2) heritabilities and values for the maternal permanent environmental effects (c^2) are shown in Table 1. For comparisons, published heritability estimates for BWT and WWT are summarised in Tables 4 and 5, respectively. Standard errors of the heritability estimates were unavailable for those estimated from Models 3 and 4, while those obtained from Models 1 and 2 were low.

The log likelihood values obtained under the four different models of analyses are shown for each trait in Table 1. In this study, fitting the maternal genetic effects as the only random effect in addition to the direct genetic effect resulted in larger log likelihood ratios than in models that ignored the maternal genetic effects. The estimates of m^2 were also larger than both the h^2 and c^2 estimates for BWT. For WWT and ADG, both the m^2 and c^2 estimates were smaller than the h^2 estimates, while they were almost equal in the model (M4) which included both simultaneously.

The h^2 estimates for BWT ranged from moderate to moderately high (h^2 = 0.19 to 0.38). In Model 1, where maternal effects were ignored, the h^2 estimates were higher and most likely biased upwards. However, fitting either or both of the maternal effects reduced the σ^2_a and h^2 estimates from 0.16 to 0.08 and from 0.38 to 0.19, respectively. Likewise, failure to take account of maternal permanent environmental effects (c^2) resulted in higher maternal genetic variances (σ^2_m) and the corresponding m^2 estimates. Thus, when the maternal permanent environmental effect (c^2) was ignored, the total variance was attributed to the maternal genetic variance (σ^2_m), probably resulting in an overestimation of m^2. Thus, it is evident that the relative values of h^2 and m^2 were greatly influenced by the model used in the analysis. The estimate of the total maternal effect ($m^2 + c^2 + 1/4h^2 + \sqrt{h^2}\sqrt{m^2}\, r_{am}$; Notter, 1998) was 0.35, which indicated that the maternal effect is more important than the direct effect.

As in BWT, h^2 estimates for WWT decreased when either of the maternal effects was fitted in the model. When the maternal permanent environmental effects (c^2) were fitted in the model, the variance due to the maternal genetic effects (σ^2_m) and the corresponding estimate of m^2 decreased. As opposed to BWT, both the maternal genetic and maternal permanent environmental effects were smaller than the direct genetic effects under all models.

For ADG, the estimates of the direct and maternal genetic and maternal permanent environmental variances followed the same pattern as for WWT, and they were of approximately similar magnitude.

Estimated correlations between the direct and maternal genetic effects (r_{am}) for all three traits are shown in Table 1. Negative values were estimated for BWT and ADG. The magnitudes of those estimates for BWT were moderate while those of ADG were close to zero. Although the estimates for WWT were positive, they were also close to zero.

Direct genetic, maternal genetic, maternal permanent environmental and residual correlations and the corresponding covariance between BWT, WWT and ADG are shown in Table 2. The direct genetic correlations between BWT and WWT and between BWT and ADG were small positive, while those between WWT and ADG was almost unity. The maternal genetic correlations between BWT and WWT, BWT and ADG and WWT and ADG were all high. The maternal permanent environmental correlation estimates between the different weight traits were also positive and high.

The estimated average maternal and direct genetic trends are presented in Figures 1 and 2 for BWT and WWT, respectively. Both maternal and direct breeding values increased throughout the study period. For BWT, there were relatively sharp drops in mean maternal breeding values in 1985 and 1996, while there was a sharp increase in the mean direct breeding value in 1996. Regarding WWT, there was a decrease in 1988 in the mean maternal breeding values and a sharp drop in the mean direct breeding values in 1996. The aggregate breeding values followed more or less the same trend as the direct breeding values during most of the study period, particularly for WWT, and for this reason they were not presented. This may be explained by the large direct genetic effect for WWT.

Table 1 Estimates of (co) variance components, genetic parameters and heritability estimates for birth weight (BWT), weaning weight (WWT) and pre-weaning average daily gain (ADG)

Model	σ^2_a	σ^2_c	σ^2_m	σ_{am}	σ^2_e	σ^2_p	h^2	c^2	m^2	r_{am}	h^2_t	Log L
BWT												
M1	0.16				0.26	0.42	0.38				0.38	9629.90
M2	0.08	0.11			0.22	0.41	0.19	0.27			0.19	9078.86
M3	0.08		0.15	- 0.03	0.23	0.43	0.19		0.38	- 0.23	0.26	14821.99
M4	0.07	0.04	0.10	- 0.02	0.22	0.41	0.19	0.10	0.25	- 0.22	0.22	14799.42
WWT												
M1	5.25				9.52	14.77	0.36				0.36	9604.73
M2	4.31	1.51			8.83	14.65	0.29	0.10			0.29	9509.85
M3	3.73		1.64	0.04	9.34	14.75	0.25		0.11	0.02	0.31	15334.04
M4	3.83	0.92	0.78	0.08	9.05	14.66	0.26	0.06	0.05	0.05	0.30	15317.49
ADG												
M1	458.37				904.31	1362.68	0.34				0.34	9606.44
M2	384.71	124.27			844.85	1353.83	0.28	0.09			0.28	9530.81
M3	355.05		136.05	- 11.85	882.19	1361.44	0.26		0.10	- 0.05	0.30	15362.81
M4	362.20	85.91	55.85	- 4.25	854.50	1354.21	0.27	0.06	0.04	- 0.03	0.28	15345.38

σ^2_a = direct genetic variance; σ^2_c = maternal permanent environmental variance; σ^2_m = maternal genetic variance; σ_{am} = direct-maternal genetic covariance; σ^2_e = residual variance; σ^2_p = phenotypic variance; Log L = log likelihood; h^2 = direct heritability; c^2 = ratio of maternal permanent environmental effect; m^2 = maternal heritability; r_{am} = direct-maternal genetic correlation; h^2_t = total heritability ; $h^2_t = (\sigma^2_a + 0.5\ \sigma^2_m + 1.5\ \sigma_{am})/\ \sigma^2_p$.

Table 2 Estimated direct genetic, maternal genetic, maternal permanent environmental and residual correlations (above diagonal) and the corresponding covariance (below diagonal) between birth weight (BWT), weaning weight (WWT) and average daily gain (ADG)

Trait	BWT	WWT	ADG
Direct genetic effects			
BWT	-	0.16	0.04
WWT	0.16	-	0.99
ADG	0.42	85.49	-
Maternal genetic effects			
BWT	-	0.93	0.60
WWT	0.20	-	0.85
ADG	0.57	1.21	-
Maternal permanent environmental effects			
BWT	-	0.89	0.82
WWT	0.08	-	0.99
ADG	0.60	2.92	-
Residual effects			
BWT	-	0.16	0.02
WWT	0.30	-	0.99
ADG	0.41	126.83	-

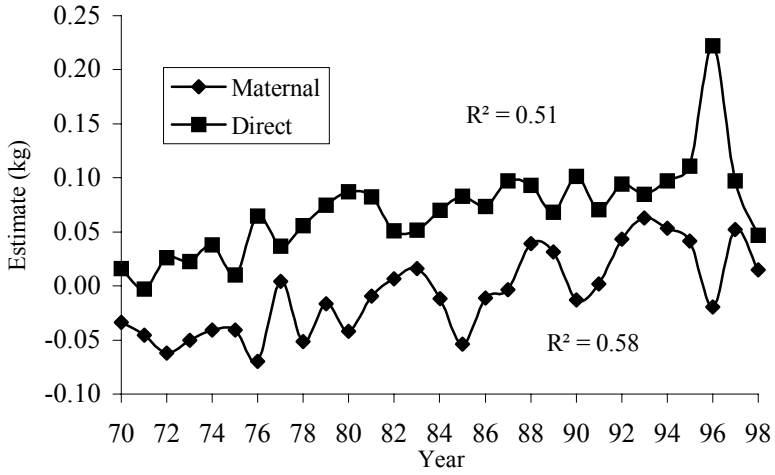

Figure 1 Regression of estimated breeding values of birth weight on year

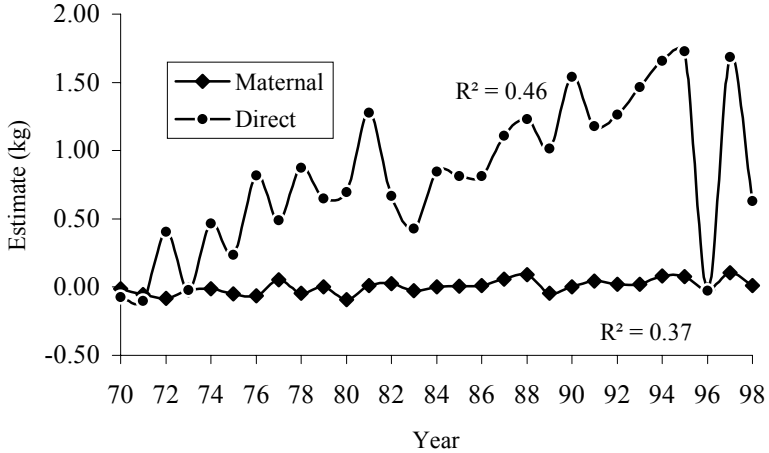

Figure 2 Regression of estimated breeding values of weaning weight on year

Discussion

Estimates of h² for BWT obtained in the present study are within the range of the animal model estimates, which varied from 0.04 (Cloete *et al*., 1998) to 0.42 (Van Wyk *et al*., 1993a; Table 3). Estimates of h² for WWT obtained from the different models were also within the ranges of published values. The h² estimates for WWT in the literature ranged from 0.09 (Burfening & Kress, 1993) to 0.50 (Fadili *et al*., 2000; Table 4). The estimates also correspond to those reported by Heydenrych (1975), which was based on part of the same data set as was used in the present study, but using sib-analysis. The estimates for ADG ranged from 0.19 (Yazdi *et al*., 1997) to 0.42 (Fadili *et al*., 2000).

Table 3 Summary of reported direct (h²), maternal genetic (m²), permanent environmental (c²) estimates and correlations between direct and maternal genetic effects (r_{am})for birth weight

Breed	h²	m²	c²	r_{am}	References
Chios	0.13-0.38	0.13-0.33	0.16-0.28	0.00 to -0.44	Ligda *et al*. (2000)
Various breeds	0.19-0.34	0.30-0.65		-0.18 to -0.74	Burfening & Kress (1993)
Horro	0.18-0.32	0.10-0.26		-0.64	Abegaz & Duguma (2000)
Elsenburg Dormer	0.16-0.42	0.43		-0.35	Van Wyk *et al*. (1993a)
Romanov	0.04	0.22	0.10	-0.99	Maria *et al*. (1993)
Hampshire	0.39	0.22	0.37	-0.56	Tosh & Kemp (1994)
Polled Dorset	0.12	0.31	0.27	-0.35	Tosh & Kemp (1994)
Romanov	0.07	0.13	0.32	-0.13	Tosh & Kemp (1994)
Swedish Finewool	0.07	0.30		0.11	Näsholm & Danell (1996)
Afrino	0.22	0.09	0.12		Snyman *et al*. (1995)
Baluchi	0.14	0.12		0.18	Yazdi *et al*. (1997)
Australian Merino	0.30	0.29		-0.43	Torshizi *et al*. (1996)
Döhne Merino	0.04	0.10	0.17		Cloete *et al*. (1998)
Moroccan Timahdit	0.18	0.59		-1.00	Fadili *et al*. (2000)
Dorper sheep	0.11	0.10	0.12	0.35	Neser *et al*. (2001)
Merino	0.18	0.15	0.08		Cloete *et al*. (2001)
Merino	**0.19-0.38**	**0.25-0.38**	**0.10-0.27**	**-0.22 to -0.23**	**Present study**

In all three traits, estimates of h² ranging from 0.19 to 0.29 were computed after maternal effects were taken into account. In contrast, failure to take account of these effects gave estimates ranging from 0.34 to 0.38. This indicates the extent to which estimates of h² can be biased if maternal effects, either genetic or environmental, are ignored using an animal model. The h² of BWT in particular was halved when either or both of the maternal effects were fitted compared to the estimate obtained under Model 1 ($h^2 = 0.38$). Several corresponding results have been reported in the literature (Torshizi *et al*., 1996; Ligda *et al*., 2000; Al-Shorepy, 2001). Snyman *et al*. (1995) reported that ignoring maternal effects, if these effects have a significant influence, leads to the over-estimation of direct as well as total heritabilities.

In the present study, the magnitude of the m² estimates obtained for BWT was greater than for both the h² and c² estimates. In some other investigations, c² also tended to be higher than both the h² and m² estimates (Table 3). In the present study, the m² estimates were, however, lower than the h² estimates for both WWT and ADG.

In general, the values for m² in the present study varied from low to medium and were influenced by the model fitted (Table 1). It accounted for about 0.38 of the phenotypic variance when the maternal permanent environmental effect was ignored from the model, but was reduced to 0.25 when the latter was fitted in the model. Snyman *et al*. (1995) also indicated that the exclusion of the maternal permanent environmental effect, when it has a significant influence, could cause estimates of m² to be biased upwards.

The maternal permanent environmental effect (c²) for BWT (Model 2) was larger than the direct genetic effect (h²), which is in accordance with results of several other studies (Table 3). The c² estimates agreed with some of the estimates reported for WWT in the literature cited (Table 4). The exception is a zero c² estimate reported by Maria *et al*. (1993). Both Snyman *et al*. (1995) and Neser *et al*. (2001) reported an estimate of 0.12, while Cloete *et al*. (2001) found an estimate of 0.07 for the

permanent environmental effect of the dam in BWT. They ascribed this value of the permanent environmental effect to the influence of the uterus and the effect of multiple births. Relatively large c^2 estimates for WWT and ADG most likely reflected differences the rearing abilities of dams that might be influenced by environmental fluctuations between years or her birth/weaning status. Literature results indicated that early growth of an ewe has an effect on the amount of milk she gives to her lambs during her early life (Gould & Whiteman, 1975).

Table 4 Summary of reported direct (h^2), maternal genetic (m^2), permanent environmental (c^2) estimates and correlations between direct and maternal genetic effects (r_{am}) for weaning weight

Breed	h^2	m^2	c^2	r_{am}	References
Chios	0.15-0.29	0.05-0.16	0.08-0.12	-0.22 to –0.26	Ligda *et al*. (2000)
Various breeds	0.09-0.22	0.07-0.48		-0.41 to –0.88	Burfening & Kress (1993)
Elsenburg Dormer	0.13-0.34	0.20		-0.16	Van Wyk *et al*. (1993a)
Horro	0.10-0.26	0.19-0.24		-0.42	Abegaz & Duguma (2000)
Romanov	0.34	0.25	0.00	-0.97	Maria *et al.* (1993)
Hampshire	0.39	0.19	0.20	-0.74	Tosh & Kemp (1994)
Polled Dorset	0.25	0.08	0.19	-0.31	Tosh & Kemp (1994)
Romanov	0.14	0.02	0.12	0.43	Tosh & Kemp (1994)
Swedish Finewool	0.12	0.13		0.47	Näsholm & Danell (1996)
Afrino	0.33	0.17			Snyman *et al*. (1995)
Baluchi	0.19	0.03		0.51	Yazdi *et al*. (1997)
Australian Merino	0.28	0.41		-0.59	Torshizi *et al*. (1996)
Moroccan Timahdit	0.50	0.24		-0.94	Fadili *et al*. (2000)
S. A. Mutton Merino	0.19	0.09	0.10	-0.55	Neser *et al*. (2000)
Dorper sheep	0.20	0.10	0.08	-0.58	Neser *et al*. (2001)
Merino	0.30	0.08	0.07		Cloete *et al*. (2001)
Merino	**0.25-0.36**	**0.05-0.11**	**0.06-0.10**	**0.02 to 0.05**	**Present study**

Generally, results showed a trend of increasing direct but decreasing maternal variance ratios from birth to weaning. The increasing h^2 of lamb weight at weaning is most likely caused by an increased expression of genes with direct effects on body development (Yazdi *et al*., 1997). This also confirms the idea of Robison (1981) and Snyman *et al*. (1995), who concluded that maternal effects in mammals diminish with age. In general, results of this study showed that maternal effects, genetic and environmental, are important for BWT and need to be considered in selection.

The correlation estimates obtained between direct and maternal genetic effects (r_{am}) for BWT are lower than most of the estimates reported in the literature cited (Tables 3). The estimate of 0.35 reported by Neser *et al*. (2001) for BWT contradicts the negative estimates found in this study. This study reported a high negative correlation estimate in WWT. In the present study, the signs of these estimates for WWT agreed with those reported by Näsholm & Danell (1996), Snyman *et al*. (1996) and Yazdi *et al* (1997). However, the positive genetic correlations ranging from 0.18 to 0.57 reported by these authors were higher than those of the present estimates, which were very small, ranging from 0.02 to 0.05. This suggested that selection for increased liveweight of the lamb would not negatively affect the maternal ability of the ewe. Cloete *et al*. (2001) also found no significant correlation between the direct and the maternal effects in another Merino flock. The estimates for ADG are slightly lower than the –0.17 reported by Van Wyk *et al*. (1993a). Yazdi *et al*. (1997) reported positive estimates ranging from 0.23 to 0.28 for ADG. A negative estimate of the direct and maternal genetic covariance has mostly been observed in field data while it has by and large been absent in experimental data sets (Meyer, 1997), whom has indicated that this could have been attributed to factors like more uniform management and lack of preferential treatment. Alternatively, it may also reflect better identification of contemporary or management groups.

Early growth traits in sheep are mostly characterised by negative r_{am} estimates (Tables 3 and 4). These estimates may be considerable and could be affected by small data sets (Maria *et al*., 1993; Fadili *et al*., 2000; Al-Shorepy, 2001), the models fitted or poor pedigree structure that is inadequate for obtaining estimates of both the direct and maternal heritabilities and the genetic correlations between animal effects (Kominakis *et al*., 1998; Lee *et al.*, 2000). Both Meyer (1992) and Swalve

(1993) suggested that environmental covariances between the dam and her offspring that are not accounted for may bias the direct and maternal genetic correlation downwards. The antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may also be due to natural selection for an intermediate optimum (Garrick *et al*., 1989; Tosh & Kemp, 1994).

Genetic correlations between growth traits obtained in this study were positive and varied from low to high (Table 2). A small direct genetic correlation was estimated between BWT and WWT. Thus, it seems that selecting for heavier WWT in this flock may possibly not result in substantial increases in BWT, though the standard error of the estimate is expected to be relatively large owing to the small data set. This might help to avoid lambing difficulties, which could result in loss of lambs and their dams. In this flock, a significant reduction in survival rate of lambs was observed as lambs became heavier (≥ 5.0 kg) at birth (Heydenrych, 1975; Duguma, 2001). The estimated maternal genetic and maternal permanent environmental correlations were all high. The nearly zero correlations observed between the direct and maternal genetic effects for WWT (Table 1) and the high maternal genetic correlations between WWT and other traits (Table 2) could indicate the likely response to selection on individual weaning weight performance. The high direct genetic correlation (r_a = 0.99) between WWT and ADG implies that they are genetically the same trait and that selection could consequently be applied on either one or the other. In the present study, even after re-examination of the data, the cause for the either sudden drop or rise of the direct and maternal genetic effects in 1985 and 1996 could not be addressed, but may be related to incorrect data recording during these particular years.

Conclusions

Heritability estimates of early growth traits from the different models ranged from moderate to moderately high. It seems that, ignoring maternal effects, both maternal genetic and environmental effects lead to an overestimation of the h^2 estimates. Likewise, exclusion of maternal permanent environmental effects of the dam resulted in overestimation of m^2 estimates, particularly for BWT. Thus, they need to be considered when carrying out genetic evaluations of early growth traits, in addition to the direct genetic effects. The absence of a genetic antagonism for WWT between the direct and the maternal genetic effects obtained, suggests that genetic improvement could be obtained in both direct and maternal performances if selection is based on individual weaning weight performance.

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